THE CHIRONOMIDAE (DIPTERA) LARVAE OF ATHERTON TABLELAND LAKES, NORTH QUEENSLAND

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The invertebrate biota of the benthos of lakes can provide an historical record of ecological (including climate) change through their preserved record in dated sediments. Such records are available through the remains of Chironomidae (Diptera) larvae recovered from lake sediments. However, to interpret the palaeo-assemblages recovered, the modern biota must be known and identifiable. Here we review, provide notes and offer an illustrated identification guide to the larval stages of Chironomidae revealed by surveys of three major Atherton Tableland lakes (Barrine, Eacham and Euramoo). Genera can be identified from variably incomplete palaeomaterial and can convey much information: here we report 8 genera belonging to the subfamily Tanypodinae, 2 to the Orthocladiinae, and 20 to Chironominae. Some are monotypic; in several genera named species can be recognised, whereas in others species-level diversity cannot be established on the basis of larval morphology. Larvae clearly identifiable as belonging to *Parakiefferiella* requires an expansion of the existing generic diagnoses in having a bifid SI seta and 3-4 short setae in a ventromental beard. Distributions outside the immediate area tend to be northern Australian to Asian, with little or no evidence of cool/mesotherm, southern-connected (temperate 'Gondwanan') taxa. ☐ *Chironomidae, larvae, north Queensland, Atherton Tableland.*

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Studies of the lakes of the Atherton Tableland in tropical North Queensland have allowed insights into the history of the area, and by extrapolation, the Australian continent. Selected biotic proxy indicators (Cohen, 2003), notably pollen, diatoms and chironomid larval head capsule subfossil remains, have been extracted from the accumulated lake benthic sediments as time-series samples to deduce past climate and assess the effects of human activities, such as fire. In contrast to pollens, chironomid larval head capsules allow near species-level determinations, and perhaps a finer control for the time of deposition with respect to the investigated time horizons.

Our studies of Chironomidae in lakes of the Atherton Tableland have concentrated on Lakes Barrine and Euramoo for palaeosediment and modern studies, and include Lake Eacham for neontological studies alone. The recent fauna is the focus of this paper, since understanding the extant fauna and its contemporary distribution on the continental-scale is fundamental to deducing past events.

Australian lacustrine Chironomidae have been investigated less intensively than those of the lotic (running waters), with no national survey. Previous Australian lacustrine studies were conducted when the taxonomic knowledge of immature stages of Australian chironomids was in its infancy. Furthermore, these studies relied upon collections of benthic larvae, often restricted to profundal sediments. Immersed wood and floating materials, attached sponges, and macrophytes were poorly sampled. We can integrate and overcome the effects of variation associated with substrate heterogeneity and diel emergence patterns through collection of pupal exuviae — the cast skin left on the water surface at adult emergence. Shoreline and nearshore accumulations of exuviae thus establish effective independence from particular larval habitats.

Previous inventories of Australian lacustrine chironomid diversity give a general impression of modest to low species-richness judged from larvae, and often greater richness based on pupae, as reviewed by Wright & Cranston (2000). In surveys of macrobenthos of Tableland lakes, Chironomidae were included only by Timms (1979) who used a Birge-Ekman grab to sample 15 stations in Lakes Barrine and Eacham and 4

stations at Lake Euramoo and reported 7 species as larvae from Lake Barrine, 8 species from Lake Eacham and none from Euramoo. Few chironomid taxa including *Procladius* Skuse, 1889 and *Chironomus nepeanensis* Skuse, 1889 were associated with the profundal and taxa such as *Cryptochironomus* Kieffer, 1918 at Lake Barrine, and *Coelopynia* Freeman, 1961 and *Cryptocladopelma* Sæther, 1971 at Lake Eacham were confined to the littoral zone. The absence of macrobenthos in the profundal of Lake Euramoo was attributed to the extremely flocculent nature of the substratum and anoxic conditions present during long periods of lake stratification (Timms, 1979). Our pilot studies of pupal exuviae at Lake Euramoo revealed a larger diversity. Subsequent collections from Eacham and intensive studies at Barrine and Euramoo to associate larvae with exuviae, and extraction of larval head capsules provided evidence of potentially over 40 shared and unique species in total. Species richness assessed by subfossil head capsules is higher than in benthic larval surveys, with taxa such as *Zavreliella marmorata* Wulp, 1859, *Thienemanniella* Kieffer, 1911, *Microchironomus* Kieffer, 1918, *Riethia* Kieffer, 1917, and ?*Skusella* sp. present only amongst subfossil assemblages.

Here we provide taxonomic substantiation to accompany reconstructions based on chironomid larval remains for Lakes Barrine (Dimitriadis & Cranston, 2001) and Euramoo (Haberle et al., unpubl. data).

MATERIALS AND METHODS

The three study sites are maar crater lakes lying between 17°10' and 17'S and 145°37' and 38'E at elevations of 720-746m a.s.l. on the Atherton Tableland, close to the current western rainforest ecotone. Lakes Barrine and Eacham are deep (67m, 63m, respectively), whereas the sampled southern basin of Euramoo is shallower at 17m. Lake Barrine has the greatest surface area (1.03km^2) more than twice the area of Eacham (0.46km^2) and Euramoo (0.4km^2). All lakes are partially to completely stratified, slightly acidic, humic and dilute. The steepness of crater slopes preclude extensive littoral swamps from Lakes Eacham and Barrine, but a more extensive zone of *Phragmites*, *Blechnum* and *Cyperus* exists at Lake Euramoo. Further details on morphology, physico-chemistry and palaeolimnological studies are provided by Walker (1999), Dimitriadis & Cranston (2001) and Haberle et al. (unpubl. data).

Sampling chironomids involved a variety of collection methods. Pupae and their exuviae were collected by nets with a 300µm mesh at the water surfaces along windward shores. Larvae were collected live from the shallow littoral zones with similar sized mesh nets. Profundal larvae were sampled by Ekman grab (e.g. Veijola et al., 1996). Palaeosediments from Lake Euramoo were collected using a modified Livingstone piston corer with a core tube diameter of 5 cm whereas sediments from Lake Barrine were recovered using a Mackereth corer.

Larval materials were collected from Lake Euramoo in June 1999, and from Lake Barrine in April and June 1997, and in April, July and October of 1998. Pupal exuviae were collected from Barrine and Lake Eacham on these sampling occasions and opportunistically on other occasions.

Isolation of 3rd and 4th instar chironomid head capsules generally followed the procedures outlined by Walker (1987, 2001). Sediment samples were deflocculated with warm water running through 60 µm mesh. Residues retained on sieves were backwashed into plastic vials and sorted in a Bogorov counting tray under 25-50 × magnification with a Wild Heerbrugg dissecting microscope. Head capsules were transferred to drops of water on cover-slips using #4 forceps. Cover-slips containing approximately 15 head capsules were dried and mounted onto glass slides with Euparal for later identification. Remains were identified under 100-400 × magnification using an Olympus BH2 compound microscope.

The association between larva, pupa and adult necessary for full taxonomic descriptions has been attempted by rearing live larvae individually through to the adult. Live larvae were placed individually in a few ml of native (or tap) water in cotton-wool stoppered 50 × 10mm glass vials, and maintained at cooler than ambient temperatures, without aeration. Any emerged adults and associated exuviae were preserved in 70% ethanol.

Microscope slide preparation involved clearing where necessary with 10% KOH, neutralisation and initiation of dehydration with glacial acetic acid, then mounting from propan-2-ol (isopropanol) into Euparal. Exuviae were displayed by dissecting the cephalothorax from the abdomen, and attempts were made to remove pharate adults from exuviae.

Voucher specimens of larvae of most species are deposited in the Queensland Museum, others and pupal exuvial specimens are in the Australian National Insect Collection, Canberra, which is the primary repository for Australian Chironomidae.

Photographs were taken with an Automontage™ system, allowing automated retention of focused parts of a sequence of exposures at different focal depths. All subsequent manipulations were made in Adobe Photoshop.

TAXONOMY

Subfamily TANYPODINAE

This subfamily comprises many genera in which the larvae are predominantly, but not exclusively predatory. Previous keys to larvae, including Wiederholm (1983), have used dimensions of the head capsule, which is fraught with error associated with variable compression, and certainly does not work for fragmentary subfossil heads, nor imperfectly prepared slide mounts. Features of the ligula (the toothed part of the hypopharynx), the paraligulae, inner teeth of the mandible and the frequently reduced mentum all assist in identification (Fig. 1A). However, Kowalyk (1985) discovered very useful variation in the position and shape of cephalic setae and sensory pits on the ventral and dorso-lateral surface of the head capsules of Tanypodinae. Although the setae often are missing or highly translucent, the relative positions of pits from which they arise have widespread utility. The arrangement of the pits of the ventral setae (SSm - seta submentum, S9, S10, cephalic setae 9 and 10) and ventral pore (or 'pit') (VP) alone provides much distinguishing detail in the tribe Pentaneurini (Cranston, 1996; 2000b), although informative variation exists amongst non-pentaneurine tanypods (e.g. Figs 1D,E; Kowalyk, 1985; Rieradevall & Brooks, 2001) and also in dorsal/dorsolateral setae and the dorsal pore. In the figures that accompany this paper, the ventral head is orientated with the anterior direction towards the top to show the setae and ventral pore of right sides.

Clinotanypus Kieffer, 1913 (Fig. 1A-D) is represented in Australia by one named species, *C. crux* Wiedemann, 1824, an Indian species recognised as Australian by Freeman (1961) based on adults from northern New South Wales and Queensland. Although larvae clearly ascribable to *Clinotanypus* are widespread in warm standing waters, rearing has proved difficult. Allocation of all these northern eurythermic larvae to the species *C. crux* is not contradicted by limited pupal exuvial or adult evidence. Larvae, pupal exuviae and rearings have been made from Lake Barrine only.

Coelopynia Freeman, 1961 (Fig. 1E,F) is a monotypic genus endemic to Australia, whose immature stages were described by Roback (1982a). *Coelopynia pruinosa* Freeman, 1961 occurs in lakes and rivers from north Queensland to Tasmania, and as far west as the Kimberley and Millstream. We found *Coelopynia* larvae only in Lake Eacham, although we have subfossil material from Lake Barrine where Timms (1979) recorded the taxon.

Fittkauimyia Karunakaran, 1969 (Fig. 1G,H) was erected for a distinctive tanypod reared from a ditch in Singapore. Roback (1982b) described the immature stages from Australia. The sole eastern hemisphere species *Fittkauimyia disparipes* Karunakaran, 1969 appears to be widespread throughout south-east Asia to Australia, where it occurs as far south as the southern and subcoastal lagoons in southernmost NSW. Larvae live in rivers and pools, and in the Northern Territory the genus tolerates high acidity and metals in polluted flow from abandoned mines (Hardwick et al., 1995) and organic, industrial and sewage contaminated lagoons (S. Dimitriadis pers. obs.). Larvae, pupal exuviae and subfossil head capsules were found in Lakes Barrine and Euramoo.

Procladius Skuse, 1889 (Fig. 1I) is a common and often abundant taxon, in which, worldwide, species-delimitation is difficult in any life-history stage. Recognition of three segregates of pupal exuviae that correspond to the described species of adults in Australia, is conservative and perhaps underestimates the diversity. Pupal exuviae of *Procladius* from Eacham and Barrine all belong to *P. squamifer* Freeman, 1961 whose larva seems indistinguishable from *P. paludicola* Skuse, 1889. In much of mid- and southern Australia these two species may co-occur, although *P. squamifer* perhaps is less tolerant of polluted conditions.

Tribe PENTANEURINI

Ablabesmyia Johannsen, 1905 (Fig. 2B,D,E) is a distinctive genus of pentaneurine tanypod, sharing with *Paramerina* Fittkau, 1962 the divided basal palp segment and having one or two claws of the posterior parapod darkened (the latter feature has been stated to be diagnostic for *Ablabesmyia* but Australian *Paramerina* may have a darkened claw, and some individuals of *Ablabesmyia* may have all claws pale). Two larval taxa of *Ablabesmyia* are distinguishable: *A. hilli* Freeman, 1961 that has the palp divided into 4 sections (Fig. 2B), and *A. notabilis* Skuse, 1889
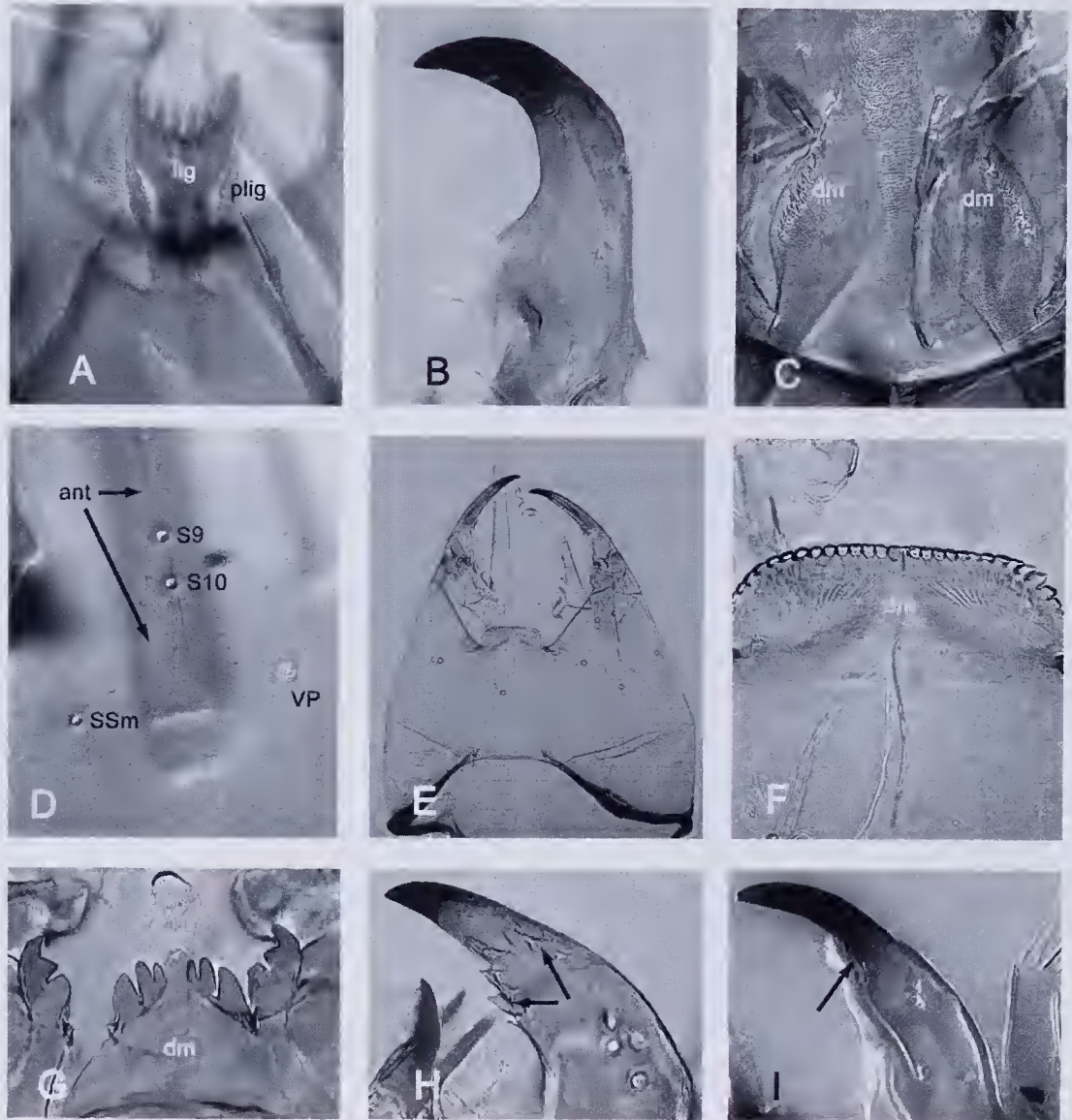
FIG. 1. A-D, *Clinotanypus crux*: A, ventral head, ligula (lig), paraligula (plig); B, mandible; C, dorsomental teeth (dm); D, antenna (ant), ventral setal pits and pore (S9, 10 - cephalic seta 9, 10, SSm - seta submentum, VP - ventral pore). E-F, *Coelopynia pruinosa*: E, ventral head. F, dorsomentum (dm). G-H, *Fittkauimyia disparipes*, G, dorsomentum (dm); H, mandible. I, *Procladius squamifer*: mandible.

with a bipartite palp. There is much variation, including in relative lengths of palp segments and intensity of pigment of the posterior parapod claws, suggesting either geographic variation or further, unrecognised, species.

Larvae identified here as belonging to *A. hilli* have only 1 dark posterior parapod claw (Fig. 2D), have 4 parts to the palp (3 of which are pigmented, the base hyaline, Fig. 2B). Only pupae have been found that may belong to *A. notabilis*, whose larva has only two parts to the palp, and 2 (or 3) dark posterior parapod claws. Separation of pupae of *A. hilli* from *A. notabilis* is difficult, relying on somewhat subjective assessment of the shape of the thoracic horn — more oval for *hilli*, more elongate in *notabilis*.
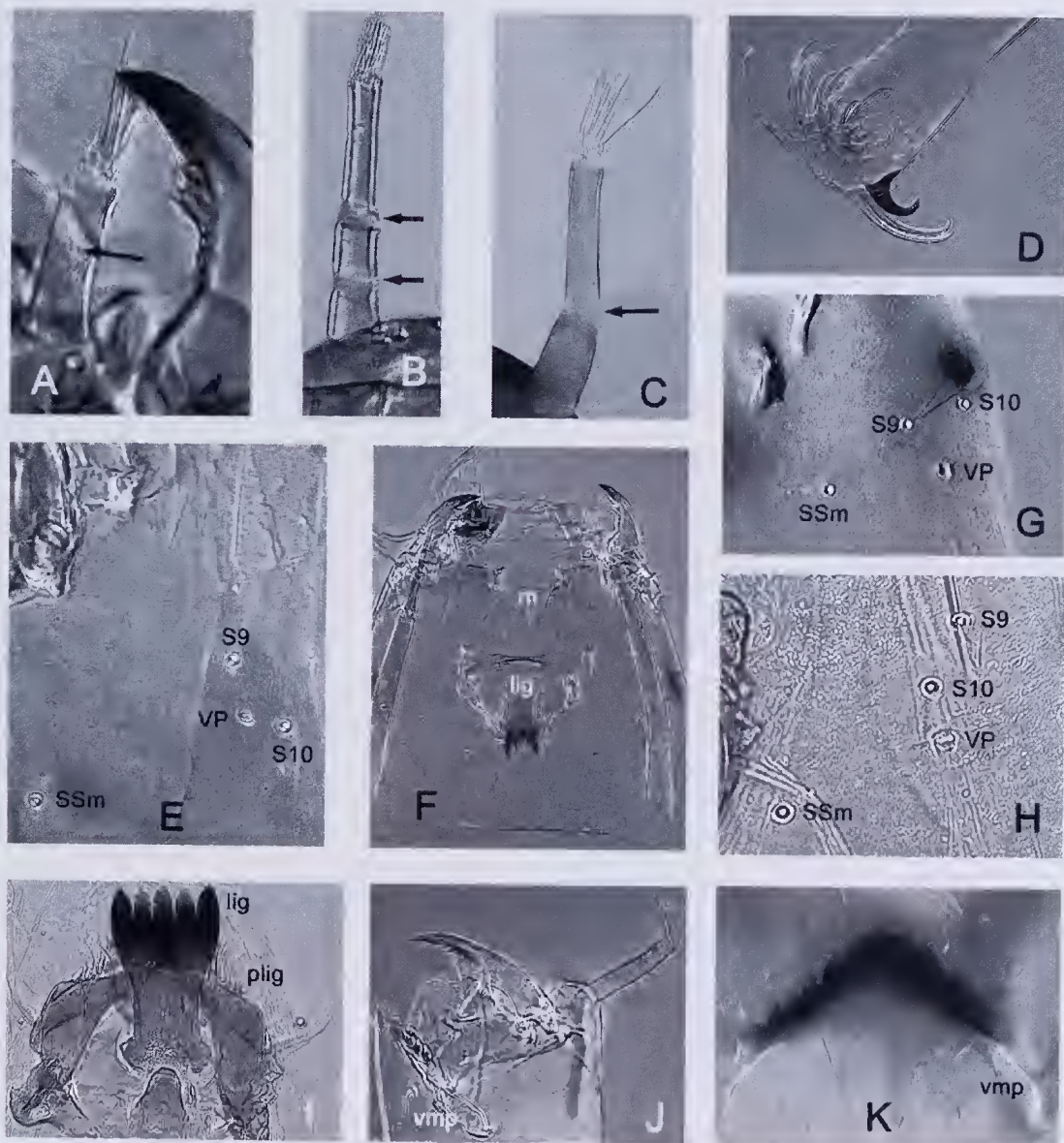
FIG. 2. A, *Monopelopia* sp.: undivided maxillary palp. B, D-E, *Ablabesmyia hilli*: B, divided (arrowed) maxillary palp. D, posterior parapod; E, ventral setal pits and pore (S9,10 - cephalic seta 9, 10, SSm - seta submentum, VP - ventral pore). C, *Paramerina* sp.: divided (arrowed) maxillary palp. F-G, *Monopelopia* sp., F, ventral head, ligula (lig), mentum (m); G, ventral setal pits and pore (S9,10 - cephalic seta 9, 10, SSm - seta submentum, VP - ventral pore). H-I, *Paramerina* sp., H, ventral setal pits and pore (S9, 10 - cephalic seta 9, 10, SSm - seta submentum, VP - ventral pore). I, ventral head, ligula (lig), paraligula (plig). J, *Nanocladius* sp, right half ventral head capsule, ventromental plate (vmp). K, *Parakiefferiella* sp., mentum and ventromental plate (vmp).

Undoubtedly *A. hilli* is the commoner species where both occur in Lakes Eacham and Barrine. Despite contemporary abundance in the two lakes, and the reported presence of the genus by Timms (1979), no subfossil material was recovered. Elsewhere both species appear to be tolerant of organic pollution and thermal stress; perhaps their recent occurrence in Atherton lakes relates to a decline in water quality.

Monopelopia Fittkau, 1962 (Fig. 2A,F,G) a pentaneurine genus, unusual amongst Australian Chironomidae in that it is recorded solely on larvae, none of which have been reared or associated with pupal or adult stages. Generally identifications of Pentancurini based upon larva alone have been uncertain, but in this case a suite of distinctive features render it certain. The inner mandibular teeth are well developed (for a pentaneurinc) (Fig. 2A), the apical 2/3 of the basal antennal segment is dark, and the ventral cephalic setae distinctively aligned (Fig. 2F,G).

Monopelopia larvae have been found in swampy shallow billabongs along the Victorian River Murray and in similar dystrophic lakes further south in the State. A larva was collected from Lake Euramoo and subfossil head capsules were abundant in the sediments.

Paramerina Fittkau, 1962 (Fig. 2C,H,I) a globally-distributed pentaneurine genus containing a swarm of species with rather little morphological differentiation in any stage. The genus is distinctive in the larva, with the basal palp segment divided into two, with the division 1/3 from the base and the ring organ in the thinner membrane between the two parts (Fig. 2C). The distribution of setal scars and pore on the ventral head is characteristic (Fig. 2H). Differentiation of species in Australia by Roback (1982a, b) was based largely on morphometries from few specimens. Size variation is now known to be great across the continental range and the basis for species segregation may be confused by unstudied allometric variation making species segregation difficult. Pupal exuviae from Lakes Barrine and Eacham appear monomorphic, with a distinctively small plastron plate on the thoracic horn. This resembles that shown by Roback (1982a,b) for *P. levidensis* Skuse, 1889 but reared (though pharatc) adults have dark wings (perhaps due only to dense dark hairs or with some pigment on the membrane) and dark smears on the thoracic pleurae unlike the adult type of *P. levidensis*. Without complete revisionary study, probably necessitating molecular data, we cannot assign the taxon to a described species. A smaller taxon, *Paramerina parva* Freeman, 1961 with a larger pupal plastron plate, is named from northern Australia. Despite *Paramerina* being quite common in contemporary Lakes Barrine and Eacham, no subfossil heads have been found, though common as subfossils at Lake Euramoo. Some *Paramerina* species are pollution-tolerant and their recent presence may indicate some deterioration in water quality in Eacham and Barrine.

Subfamily ORTHOCLADIINAE

Orthocladiinae is speciose in Australia, as elsewhere, in a diversity of larval habits especially lotic ones. Cold, oxygenated lakes have much higher orthoclad diversity than warm, oxygen-depleted ones. That only two taxa are present in modern Atherton lakes is surprising, as is the lack of species of the eurytopie genus *Cricotopus* Wulp, 1874. This latter absence seems genuine — no exuviae or subfossil head capsules of this genus were found in any site studied. We can provide no explanation for this, because one to several species of these algal grazers are expected in any tropical billabong thus far studied. The only orthoclad taxon additional to those mentioned below is *Thienemanniella* Kieffer, 1911 found as a 2000-1000 yr subfossil from Lake Barrine. Generic concepts agree with those in Wiederholm (1983) and Cranston (1996, 2000b) except for some details in *Parakiefferiella* Thienemann, 1936 (q.v.).

Nanocladius Kieffer, 1913 (Fig. 2J) is a world-wide distributed genus, modestly speciose in the Holarctic, with a less well known, perhaps less diverse, southern continental distribution. In Australia two speeies are known from Western Australia, while in the east what appears to be a single species is widespread in running and standing waters. Few rearings exist to test the species concept, but apparently the same unnamed species is figured by Cranston (1996) as *Nanocladius* sp. The pupa keys to the bicolor group in the Holarctic guide (Coffman et al., 1986).

Parakiefferiella Thienemann, 1936 (Fig. 2K) is a worldwide genus which presents a wealth of morphological features of larvae and pupae that can allow species segregation. Nevertheless, although four pupal exuvial types have been recognised in Australia (Cranston, 1996) no species are described formally yet. The generic diagnosis for larval *Parakiefferiella* in Wiederholm (1983) has to be emended to incorporate some unusual features exhibited by this undescribed Australian taxon: there is a ventromental beard of 3-4 short but distinct setae, and the S1 seta on the labrum is bifid.

Subfamily CHIRONOMINAE

Species of this subfamily always are dominant in warm standing waters. The apparently universal presence of haemoglobin in the larva allows uptake of oxygen from warm, oxygen-depleted benthic waters. As expected, the diversity of this

subfamily is high in the lakes of the Atherton Tableland, with 20 genera reported. *Zavreliella* Kieffer, 1920, *Microchironomus* and *Riethia*, recorded as subfossils were not found in modern collections. Two diverse genera, *Polypedilum* Kieffer and *Tanytarsus* v.d. Wulp, are problematic to identify as larvae and the treatment here remains incomplete. Generic concepts agree with those in Wiederholm (1983) and Cranston (1996, 2000b).

Tribe CHIRONOMINI

Chironomus Meigen, 1803 (Fig. 3A,B) is a worldwide genus with many species described predominantly on adult male genitalia and on distinctive cytology. Isolated larval head capsules cannot be identified reliably to species, and the variation in pupal exuviae has yet to be associated with named species. *Chironomus* larvae and pupal exuviae have been recovered from most tableland lakes on most sampling occasions, but numbers have never been high. Timms (1979) reported *Chironomus nepeanensis* Skuse, 1889 from both Eacham and Barrine, identified by Jon Martin and therefore reliable. To our eye, only one morphotype was present, probably attributable to *C. nepeanensis*.

Cladopelma Kieffer, 1921(Fig. 3C) is a globally-distributed genus. In Australia, only *C. curtivalva* Kieffer, 1917 has been recognised. Although there is much morphological variation in the pupa, especially in the shape of the spur ('comb') on the posterolateral of segment VIII, as yet no discrete units that may be species can be segregated. *Cladopelma* has been found as a modern exuviae from Lake Eacham, and as a subfossil larva from Barrine.

Conochironomus Freeman, 1955 (Fig. 3D) is distributed in Africa, southeast Asia and Australia. Larvae have a six-segmented antenna with Lauterborn organs alternate on the apices of segments 2 and 3, and a uni-coloured brown mentum with four subequal median ventromental teeth delimited (Fig.3D). The genus was revised for Australia (Cranston & Hare, 1995) in all life history stages. Larval *Conochironomus* have been reported from L. Barrine (Timms, 1979) from which lake we have identified larvae of *Conochironomus cygnus* Cranston & Hare, 1995 from 6m depth. The genus exists also as subfossils in L. Barrine, and as exuviae from L. Eacham. *C. cygnus* is reported previously from Blue Lake on North Stradbroke Island, numerous streams and billabongs in the Kakadu area

(Northern Territory), and the Fitzroy River in the Kimberley of Western Australia. Since Cranston & Hare (1995), more southerly distributions to southernmost subcoastal NSW have been revealed, in shallow, summer-warm waters.

Cryptochironomus Kieffer, 1918 (Fig. 3E) is a globally-distributed genus. In Australia, only *C. griseidorsum* Kieffer, 1917 has been recognised from nearly throughout the continent. Although there is much morphological variation in all life history stages, as yet no coherent units that may be discrete species have been segregated. Thus we treat all *Cryptochironomus* as belonging to the one described species. Larval *Cryptochironomus* have been reported from Lake Barrine (Timms, 1979) and we have identified pupal exuviae from Lake Eacham and from Barrine as contemporary and subfossil larvae.

Dicrotendipes Kieffer, 1913 (Fig. 3F,G,H) is a globally-distributed genus, with a quite speciose radiation in Australia. As a larva the genus is distinctive by the squat ventromental plates, and frequent presence of a 'fenestra' on the anterior frontoclypeus on the dorsal head. Provisional keys to larvae and pupae in Cranston (1996) allows identification of two species in the Atherton lakes. Larval *Dicrotendipes* have been reported previously from Lake Barrine (Timms, 1979) and we have identified larvae and pupae of *Dicrotendipes flexus* Johannsen, 1932 from Lakes Eacham and Barrine as contemporary and subfossil larvae. In Euramoo, *Dicrotendipes jobetus* Epler, 1988 is abundant as contemporary larvae and as subfossil head capsules. *D. jobetus* is an essentially northern and central Australian species, found predominantly in warm standing waters. *D. flexus* is similarly northern and lentic, but with a narrower distribution that does not include central Australian waters. *D. flexus* is known outside Australia from much of south-east Asia, where it is tolerant of some eutrophication.

The two species can be separated as larvae based on the mandible of *D. jobetus* having strong crenulations on the outer margin (Fig. 3H) and the possession of a strong fenestra (oval cuticular thinning) (Fig. 3G). *D. flexus* has a very faint fenestra and smooth outer mandible. These features will not separate all possible regional *Dicrotendipes* species for which Cranston (2000b) should be consulted.

Evidently *Dicrotendipes* is diverse regionally, since nearby artificial Emerald Dam has *D. balciunasi* Epler, 1988 and *D.* sp. 'K3' as well as *D. jobetus*. The identity of the species of larval
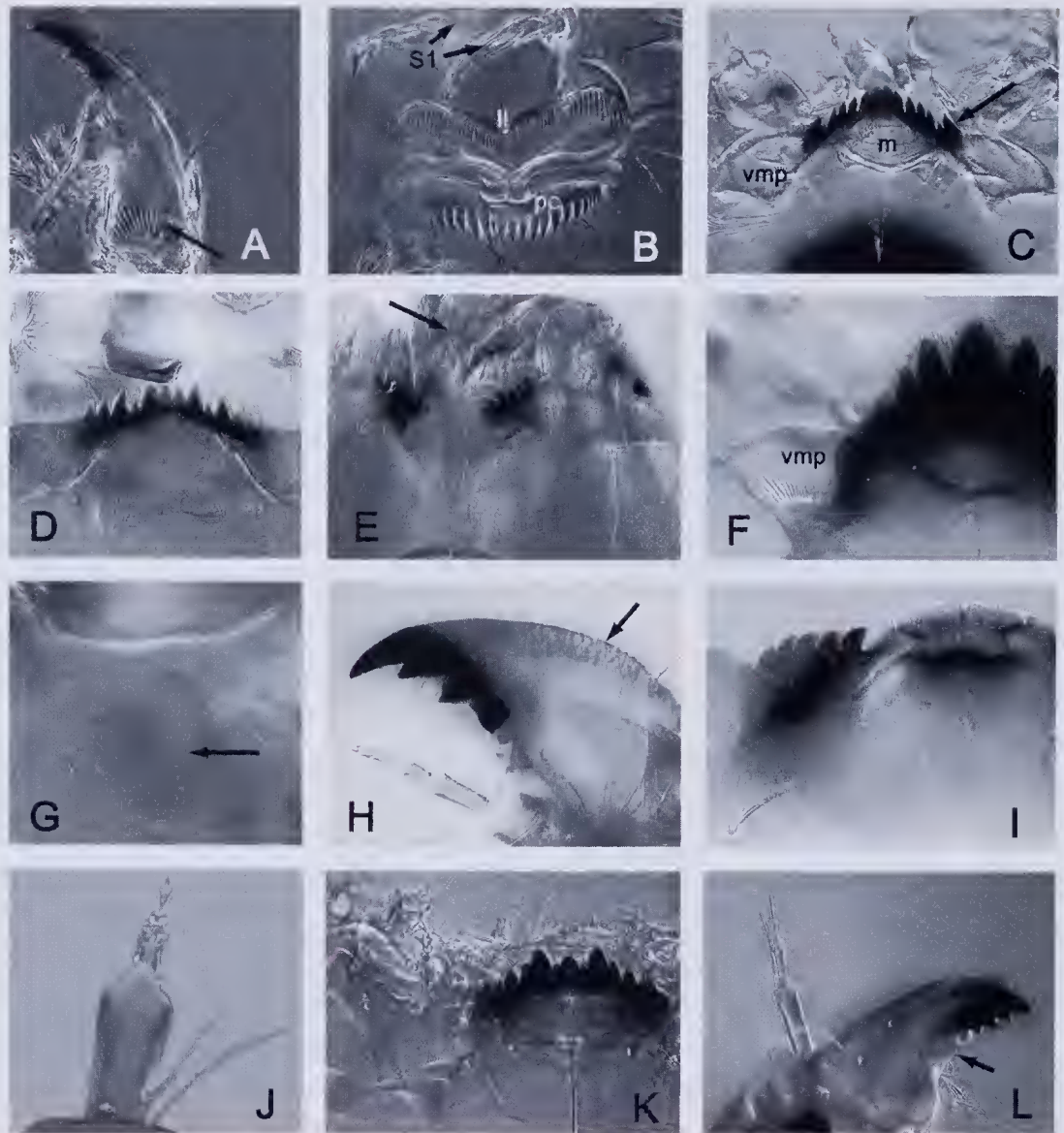
FIG. 3. A-B, *Chironomus* sp., A, mandible with basal furrows (arrowed). B, labral lamellae (ll), pecten epipharyngis (pe) and setae. C, *Cladopelma curtivalva*, mentum (m), ventromental plates (vpl). D, *Conochironomus cygnus*, mentum, ventromental plates. E, *Cryptochironomus griseidorsum*, mentum, ventromental plates. F-H, *Dicrotendipes jobetus*, F, half mentum and ventromental plate (vmp); G, dorsal fenestra (arrowed); H, mandible. I, *Harnischia* sp., half mentum and ventromental plate. J, *Harrisius* sp., antennal segments. K-L, *Kiefferulus* 'tinctus', K. mentum, ventromental plate; L, mandible, antenna.

Dicrotendipes recorded from Lake Eacham by Timms (1979) is unknown.

Harnischia Kieffer, 1921 (Fig. 3I) is represented in Australia by *H. curtilamellata* Malloch, 1915 a species described from North America, based on its proposed senior synonymy with *Cryptochironomus dycei* Freeman, 1961. Without detailed comparative study and revision of the genus on a global scale, this identification is accepted. The taxon is reported from the

Atherton lakes from exuviae only, from Lakes Barrine and Eacham. The genus is widespread in Australia especially in sandy-bedded rivers.

Harrisius Freeman, 1959 (Fig. 3J) larvae mine in wood or leaf packs and occur principally in running waters but sporadically in lakes. Pupal exuviae were found in Lake Eacham, but larvae have not yet been found in any Atherton lake. Larvae closely resemble those of another wood-mining genus, *Stenochironomus*. Principal distinction appears to be in antennal segment lengths, in which antennal segment 3 of *Harrisius* is half the length of the 4th (Fig. 3J), whereas in Australian *Stenochironomus* the 3rd appears subequal to the 4th (not illustrated through lack of specimens for photography). Distribution is sporadic along the east coast of Australia.

Kiefferulus Goetghebuer, 1922 (Figs 3K,L; 4A,B) is a diverse, worldwide genus. Larval *Kiefferulus* can be recognised by the multi-toothed premandible (Fig. 4B) and characteristic mentum (Figs 3K, 4B). Four larval morpho-types are known from Australia, one certainly comprising 3 cryptic species, *Kiefferulus cornishi* Martin 1996, *Kiefferulus intertinctus* (Skuse, 1889) and *Kiefferulus paratinctus* Martin, 1964 (a composite referred to here as *K.* 'tinctus'). Compared with previous works on Australian *Kiefferulus* (Cranston et. al., 1990; Cranston, 1996), here *Kiefferulus calligaster* (Kieffer, 1911) replaces *Kiefferulus tumidus* Johannsen, 1932 and *Kiefferulus barbitarsis* (Kieffer, 1911) replaces *Kiefferulus tainanus* Kieffer, 1912, both being senior subjective synonyms. Amongst other recorded taxa *Kiefferulus longilobus* Kieffer, 1916 is restricted to saline subcoastal habitats and *K. barbitarsis* has not been recorded from Atherton lakes. Distinctive *Kiefferulus martini* Freeman, 1961 resembles a species of *Xeno-chironomus* Kieffer, 1921 (Fig. 5C) in having a brush of long labral setae, and may be expected in certain Tableland lakes.

Two species of *Kiefferulus* co-occur in modern Lake Euramoo: *K.* 'tinctus' and *K. calligaster,* but only larvae of the former were found as subfossils. *K. calligaster* is distinguished on the mandible, which has a molar bulge (arrowed, Fig. 4A) rather than the straight mola of 'tinctus' (arrowed, Fig. 3L). The bulging outer mentum of *calligaster* (Fig, 4B) compares to the almost straight margin in 'tinctus' (Fig. 3K).

K. 'tinctus' is widespread in Australia from Kakadu to Tasmania, whereas *K. calligaster* is a northern species, extending from tropical Australia to India and south Japan.

Microtendipes Kieffer, 1915 (Fig. 4C,D) is recorded from Australia based on the reported presence of the African species *M. umbrosus* Freeman, 1955. With the present state of knowledge of the genus, this determination is accepted. *M. umbrosus* larvae, subfossils and rearings have been made from Lake Barrine, exuviae collected from L. Eacham and subfossils recovered from sediments of Lake Euramoo. Distribution in Australia seems restricted to Queensland, where previous records include abundance in experimentally-polluted channels west of Brisbane (P.S. Cranston, pers. obs.).

Parachironomus Lenz, 1921 (Fig. 4E,F) is a world-wide genus represented in Australia by several predominantly undescribed species, based on few rearings but a diversity of exuvial types. Two exuvial morphotypes are known from the region, 'K1' and 'K2', each recognised previously from surveys in Kakadu, and both found in Lake Barrine. One larval type associated tentatively with 'K2' was found as a subfossil in Lake Euramoo.

Polypedilum Kieffer, 1912 (Fig. 4G-J) is a diverse genus worldwide, and Australia is no exception. Species are differentiated primarily on male genitalia, with pupal exuviae sometimes providing confirmatory support. Larvae are less well differentiated, and features such as mentum shape, ventromental plate structure and mandibular tooth number and shape tend to be variations on a theme, with seemingly much convergence. The relative lengths of the apical 3 antennal segments provide additional discriminatory features but antennae rarely are available on subfossils. For the tableland lakes, definite identifications have been made for 7 species, of which 3 are illustrated here (Fig. 4G-J).

Although a subgeneric structure is available in *Polypedilum* it is not possible to place the immature stages unambiguously. Users are directed to an updatable web-based key (Cranston, 2000b) for guidance in identification. In Australian keys to immature *Polypedilum* (Cranston, 1996, modified in Cranston, 2000b) the taxa are keyed without reference to subgenera, although the framework is used here to discuss the species.

In the nominate subgenus, *Polypedilum seorsum* Skuse, 1889, *Polypedilum vespertinum* Skuse, 1889 and *Polypedilum watsoni* Freeman, 1961 were found as pupal exuviae in at least one
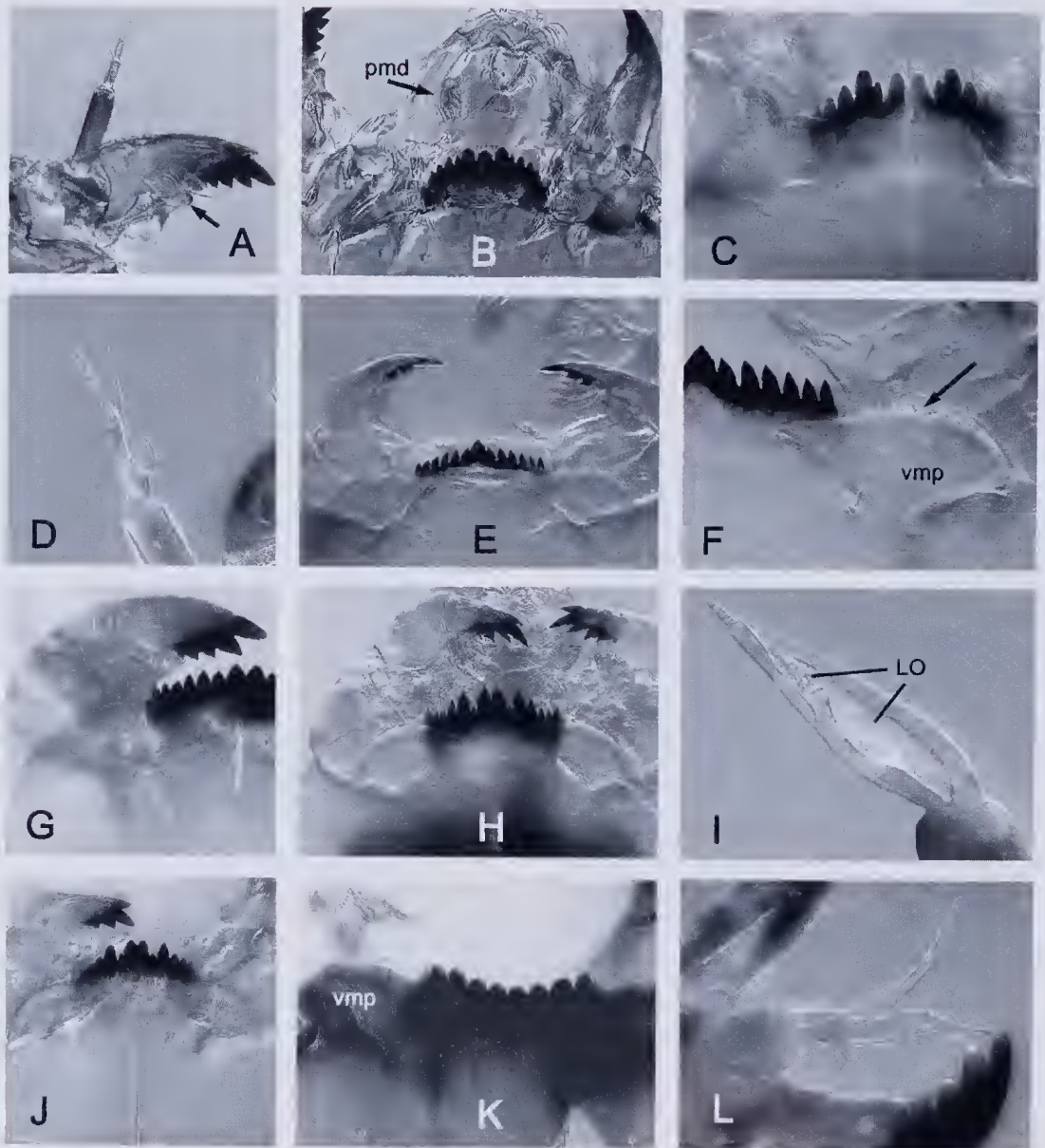
FIG. 4. A-B, *Kiefferulus calligaster*, A, mandible, antenna; B, mentum, ventromental plates, premandible (pmd). C-D, *Microtendipes umbrosus*, C, mentum, ventromental plates; D, antenna. E-F, *Parachironomus* sp., E, ventral head; F, mentum, ventromental plates (vmp), crenulated anterior margin arrowed. G, *Polypedilum leei*, half mentum, ventromental plate. H-I, *Polypedilum nubifer*, H, mentum, ventromental plate; I, antenna, Lauterborn organs (LO). J, *Polypedilum seorsum*, mentum, ventromental plate. K, *Stenochironomus watsoni*, mentum, ventromental plates (vmp). L, *Stictochironomus fluviatilis*, mandible and antenna.

regional lake, with *P. watsoni* recognised as a larval subfossil from Barrine and *P. seorsum* from Euramoo.

Three species of the likely paraphyletic or even polyphyletic subgenus *Pentapedilum* Kieffer, 1913 (Sæther & Sundal, 1999) occur in the tableland lakes: *Polypedilum (Pentapedilum) leei*

Freeman, 1961, *Polypedilum (Pentapedilum) convexum* Johannsen, 1932 and *Polypedilum (Pentapedilum)* 'K1' (Cranston, 1996). All three were present in Lakes Barrine, Eacham and Euramoo, and as larval subfossils in Euramoo and Barrine.

Polypedilum nubifer Skuse, 1889, the atypical but genotype species, was found only as a pupal exuviae in Lake Eacham. The species is typical of highly eutrophic and disturbed habitats, and may be a very recent colonist with no prior existence.

Subfossil larval head capsules that appear on the isolated menta to be close to *Polypedilum* species 'S1' and *P. prasiogaster* have been found in Euramoo and Eacham respectively, apparently without modern representation as assessed by pupal exuviae.

Stenochironomus Kieffer, 1919 (Fig. 4K) is a worldwide genus, particularly associated as larvae with immersed wood and leaves, either as a miner or grazer. *Stenochironomus watsoni* is a common, even ubiquitous species, with a characteristic larva that mines in wood. *S. watsoni* was found as a pupal exuviae and subfossil at Lake Barrine, as exuviae only at Eacham, and apparently absent from Lake Euramoo at any time. Although some immersed wood was examined, no larvae were found, as with the other wood-miner, *Harrisius* sp.

Stictochironomus Kieffer, 1919 (Figs 4L, 5A) is a worldwide genus, represented with certainty in Australia by *S. fluviatilis* (Skuse, 1889). A second species, *Stictochironomus illawara* Freeman, 1961, does not conform well to the larval generic diagnosis. *S. fluviatilis* is reported from sediments in rivers, from Arnhem Land to southern NSW, with rather few exuvial records from lakes. We have a single larva from Lake Barrine, without exuviae or subfossil material.

Xenochironomus Kieffer, 1921 (Fig. 5B,C) species are miners in aquatic sponges as larvae. This results in highly worn mouthparts, and difficulty in associating larvae with the several recognised pupal forms. Three pupal types illustrated in Cranston (1996) have been found in the Atherton lakes: *Xenochironomus* 'S1', *X.* 'K3' from Eacham and *X.* 'K4' from Barrine. Two excellently preserved larvae, without the usual sponge-spicule induced wear and with fluid gut-contents, were associated with rotting reeds in Lake Euramoo. Since none were found associated with encrusting sponges at this site, it is possible that Australian *Xenochironomus* include non-sponge-miners.

Unknown genus 'K2' (Fig. 5D,E), a distinctive pupa belonging to an undescribed taxon and recorded under the code 'unknown genus K2' in Cranston (1996) was found as exuviae in Lakes Barrine and Eacham. The larva recently associated with the 'K2' pupa was recognised as '?*Stictochironomus*'. Earlier records of exuviae were from the Kakadu/Arnhemland area of Northern Territory, predominantly from larger rivers but including some seasonally-flowing billabongs. More recent material comes from Western Australia: the Hamersleys (Fortescue Falls), north-central (Millstream, a large pool) and the south-west (a forested creek in jarrah country). Elsewhere in Queensland the taxon has been found in Cooloola National Park at Harry's Landing, and Lawn Hill National Park at Louie Creek. A southern outlier is represented by an associated larva and pupa from the Nepean River south of Sydney in NSW. A second species is represented by exuviae from the Brindabella Hills west of Canberra.

Tribe TANYTARSINI

Cladotanytarsus Kieffer, 1921 (Fig. 5F) is a worldwide genus, which is moderately species-rich in Australia, with larvae found in all types of water bodies including depositionary and brackish waters. Variation in pupal exuvial morphology suggests the existence of more species than are described, but full life history rearings necessary for associations remain too few. Only one pupal exuviae, resembling *C. bilinearis* Glover, 1973 was found at Lake Eacham; subfossils tentatively identified as this taxon were recovered from Lake Barrine.

Paratanytarsus Thienemann & Bause, 1913 (Fig. 5G,H) is a world-wide genus, and is widespread and moderately species-rich in Australia, with exuviae found in all types of water bodies. Larvae are encountered less frequently, and may inhabit typically under-sampled microhabitats. In Atherton lake surveys, only one species, *Paratanytarsus kathleenae* Glover, 1973 has been found, and only as pupal exuviae. The genus closely resembles *Tanytarsus* Wulp, 1874 and can be recognised by the pecten epipharyngis of the epipharynx comprising 3-5 finger-like lobes. Short Lauterborn organs situated on short or sessile pedestals separate nearly all species from those of *Tanytarsus* excepting an undescribed North American species (T. Ekrem, pers.
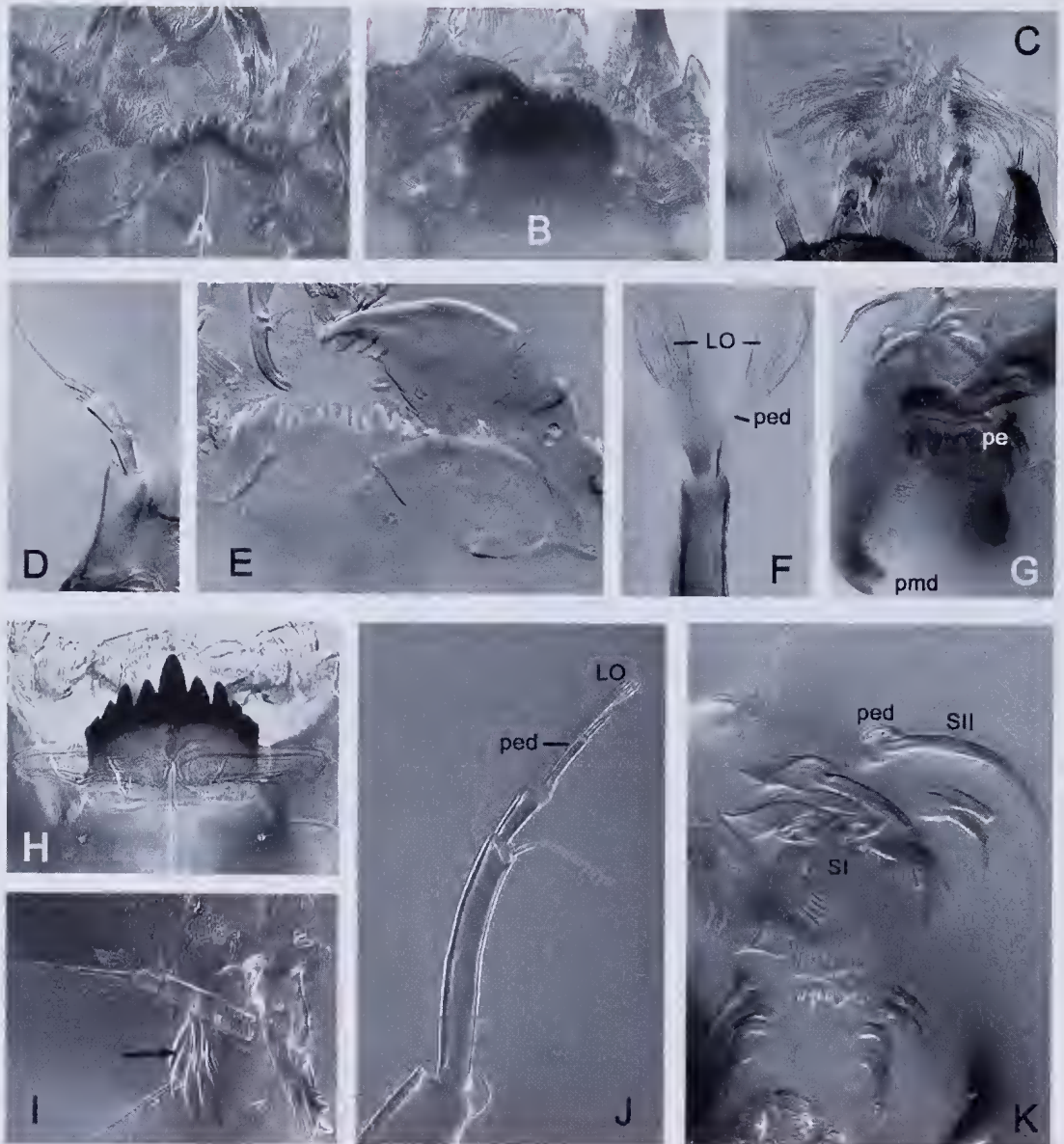
FIG. 5. A, *Stictochironomus fluviatilis*, mentum, ventromental plates, pectien epipharyngis. B-C, *Xenochironomus* sp., B, mentum; C, labrum. D-E, Unknown genus 'K2', D, antenna; E, mentum. F, *Cladotanytarsus* sp., antenna: Lauterborn organ (LO), pedestal (ped). G, *Paratanytarsus kathleenae*, labrum: pecten epipharyngis (pe), premandible (pmd). H, *Paratanytarsus* unknown species 'Euramoo', mentum and ventromental plates. I, *Stempellina australiensis*, palmate lobe at base of antenna. J-K, *Tanytarsus wendyleei*, J, antenna: Lauterborn organ (LO), pedestal (ped); K, labrum and palatum.

comm.). In subfossil material in which these features usually are missing, larval separation from *Tanytarsus* on mentum and ventromental plate structure is probably unreliable. Outside Lakes Eacham and Barrine, *P. kathleenae* is known from streams in south Queensland, and lakes, streams and rivers as far south as the subalpine area of Tasmania.

From Lake Euramoo a single larval *Paratanytarsus* recovered from decomposing reeds is distinctive

from other known congeneric larvae by the elongate median mental tooth (Fig. 5H). The only other *Paratanytarsus* from the Atherton area is a single pupal exuviae that can be allocated to no previously recognised pupal taxon (Cranston, 1996). Tergite III has posterior paired 'curtains' of posteriorly-directed fine spines, longer and denser and more transversely aligned compared to *P. kathleenae*; tergites IV and V have paired anterior spine patches resembling those of *Rheotanytarsus*. There is no spur or comb on the posterolateral corner of segment VIII.

Rheotanytarsus Thienemann & Bause, 1913 is represented in samples from Atherton only by 1 exuviae from Lake Eacham, identified using Cranston (1997) as *R. trivittatus* Johannsen, 1932. The species is known only from lotic situations from Thailand southwards to northern Victoria. No larvae have been found in lake benthos and the sole lacustrine exuviae is likely to have been a contaminant from lotic inflow, and thus no illustration is provided.

Stempellina Thienemann & Bause, 1913 (Fig. 5I) is represented in Australia by two described species: *S. australiensis* Freeman, 1961 and *S. johni* Glover, 1973. Pupal exuvial evidence and few rearings to the adult male with apparently diagnostic hypopygia suggest that this may under-represent the Australian diversity of this worldwide genus. Nevertheless, all pupal exuviae from Atherton appear to represent one species, *S. australiensis*. This taxon, figured in Cranston (1996) as *S. ?australiensis*, in the exuviae has a tapering tubular thoracic horn with few spines, a densely rugose anterior half of the thorax including two swollen tuberculose protuberances on the antero-lateral thorax. Tergal spinulation includes a medio-posterior patch of fine spinules on II just anterior to the hook row, large spinules laterally-directed only on V, and few aligned spinules on VI.

The genus is restricted to Eacham amongst surveyed lakes, but otherwise is widespread in many types of waterbodies in Australia. Larvae were not found in the neontological survey, but can be recognised easily by the palmate process on the antennal pedicel (Fig. 5I).

Tanytarsus v.d. Wulp, 1874 (Fig. 5J,K) is rich in species that are separated readily on pupal exuvial and male hypopygial features. Larvae are rather homogeneous and often are difficult to separate. Tabulated variation in antennal features, cephalic seta S3, pigment of head, mentum and

anal setae and pectination of posterior parapod claws (Cranston, 2000a) allows separation of 'monsoonal tropical' Australian species of the genus, but the utility of permutations of these features on a continental scale is untested. Furthermore, identifications of subfossil material, usually rely only on the mentum and ventromental plates, and these structures show rather minimal informative variation compared to features such as the antenna that are rarely preserved.

Tanytarsus wendyleei Cranston, 2000. Described as pupa and adult only from Northern Territory, originally as *Tanytarsus* sp. 'K4' (e.g. Cranston, 1996). Recorded from Lake Euramoo here on the basis of a common larva, one of which contains a pharate pupa identical in all observable features to *T. wendyleei*, namely with paired spinule patches on the antero-median of tergites II-VI with minimal other armament on the tergites, with 1 taeniate seta posterolaterally on VI, 2 anterior and one posterior on VII and 5LS on VIII, with a dense cluster of moderate-sized teeth on the 'comb' (posterolateral corner of VIII) (see Cranston, 2000a).

The associated larva (Fig. 5J,K), which was not known to Cranston (1996, 2000a), has a yellow head capsule without darkened occipital margin; mentum yellow brown, with darkened band across mentum at bases of teeth; cephalic seta S3 stout and simple, antennal pedestal without spur; antenna shorter than head, with segments golden, fully sclerotised excepting 2nd with only apical 20% unpigmented, with stout Lauterborn organ pedestals extending beyond antennal apex by 2/3 length of 3 terminal antennal segments, with Lauterborn organs, short and scarcely broader than pedestal. The posterior parapod claws are all simple, and the procercus is squat and gold/brown, with golden apical setae.

Tanytarsus gulungul Cranston, 2000. Described from Northern Territory, Queensland and northwestern Western Australia, originally as *Tanytarsus* sp. 'K1' (e.g. Cranston, 1996). Recorded from pupal exuviae from Lake Eacham. The larva has not been recognised from Atherton lakes, but according to Cranston (2000a) may be recognisable by: antenna only slightly shorter than head, segment 2 pigmented only in sub-basal ring, apical segments 3-5 very pale, with Lauterborn organ stems extending well beyond antennal apex, and bearing short Lauterborn organs; with cephalic S3 seta long and simple; posterior parapod claws semipectinate.

T. gulungul seems to be associated with streams and large rivers; however, although this record from Eacham is the first from a lake, several tropical 'river' sites are almost lentic after the monsoonal flow diminishes.

Tanytarsus formosanus Kieffer, 1912. Reported previously in Australia as *Tanytarsus dycei* Glover, 1973, recognised recently by Ekrem (2001) as a junior synonym of the very widespread Old World *T. formosanus*. Recorded from a pupal exuviae from Lake Eacham; abundant in Emerald Creek Dam (17°03'S 145°30'E). The larva has not been recognised from Atherton lakes, but according to Ekrem (2001) may be recognised by the antenna being short (0.6 × head length), with all segments pigmented, with short stout Lauterborn organ stems not extending to apex of antenna, bearing short Lauterborn organs; S3 simple; posterior parapod claws simple.

In Australia, *T. formosanus* is essentially tropical to subtropical, from Northern Territory, and south to Brisbane in Queensland. Apparently tolerant of nutrient enrichment and experimental pesticide addition to slowly flowing water in experimental channels.

KEY TO SUBFAMILIES OF LARVAL CHIRONOMIDAE FROM TABLELAND LAKES

1. Antenna retractile into head (Figs 1D, arrowed, 1E, 2F). Hypopharynx with distinctive toothed ligula (Figs 1A, 2I), mentum often weakly sclerotised (Figs 1A, 2F) . . . . Tanypodinae
   Antenna non-retractile (Figs 2J, 5D). Mentum a strongly sclerotised plate (the main mouthpart) (Figs 2K, 3C, 4C), with hypopharynx lacking strong ligula 2

2. Mentum associated with variably developed, but always broad and usually striated ventromental plates (Fig. 4C) . . . . Chironominae
   Mentum without, or at most with relatively small, non-striate ventromental plates (Fig. 2J,K) . Orthocladiinae

SUBFAMILY TANYPODINAE

1. Body segments bearing longitudinal lateral dense setal fringe. Dorsomentum distinct, toothed (Fig. 1E-G) . . 2
   Body segments lacking setal fringe. Dorsomentum indistinct, not toothed (Fig. 2F) . . . . tribe Pentaneurini 5

2. Dorsomental teeth not aligned on plate (Fig. 1C). Mandible strongly hooked (Fig. 1B) . . . . Clinotanypus
   Dorsomental teeth at margin of plate (Fig. 1E,F). Mandible straight to curved, never hooked (Fig. 1E,H,I). 3

3. Dorsomentum a complete arc of subequal-sized teeth amongst which median appendage is not demarcated (Fig. 1E,F) . . . . Coelopynia
   Dorsomental teeth medially interrupted by variably broad median pale median appendage (Fig. 1G) 4

4. Mandible with multiple spine-like teeth on mesal surface, without distinct basal tooth (Fig. 1H, arrowed) . . . . Fittkauimyia
   Mandible without subapical spine-like teeth (Fig. 1I, arrowed) . . . . Procladius

5. Base of maxillary palp undivided (Fig. 2A) . Monopelopia
   Basal segment of maxillary palp divided into two or more sections (Fig. 2B,C, arrowed) 6

6. One or more claws of posterior leg darker than remainder (Fig. 2D). Basal palp segment divided into 2-5 sections (Fig. 2B, arrowed); if only 2 sections, then membranous part anterior to basal 1/3. Submentum with SSm nearly aligned with VP and S_{10}, with S_9 anteromedial to alignment (Fig. 2E). . . . . Ablabesmyia
   All hind proleg claws yellow. Membranous division of maxillary palp about 1/3 from base (Fig. 2C, arrowed). Submentum with seta S_9 linearly aligned with S_{Sm} and S_{10}, with VP lying more posterolateral (Fig. 2H) . . . . Paramerina

SUBFAMILY ORTHOCLADIINAE

1. Ventromental plates extending just lateral of outermost mental tooth; mentum black (Fig. 2K) . Parakiefferiella
   Ventromental plates extending more strongly lateral and posterior to base of outermost mental tooth; mentum paler (Fig. 2J) . . . . Nanocladius

SUBFAMILY CHIRONOMINAE

1. Bases of SI setae fused and SII on long pedestal (Fig. 5K). Antenna always with 5 segments with Lauterborn organs distinct, sometimes on pedestals (Fig. 5J). Tanytarsini 2
   Bases of SI separate (Fig. 3B), SII rarely on pedestal. Antenna may be six segmented and Lauterborn organs alternate (Fig. 4I, arrowed, 4L), though usually opposite, sometimes indistinct (Fig. 3J,L). 5

2. Palmate lobe at base of antenna (Fig. 5I, arrowed); Head capsule very granular . . . . Stempellina
   No palmate lobe at base of antenna. Head capsule smooth, non-granular 3

3. Premandible bifid (Fig. 5G). . . . . . . Paratanytarsus
   Premandible with more than two teeth (Fig. 5K) 4

4. Second antennal segment cylindrical, longer than third; small Lauterborn organs arise from long pedicels (Fig. 5J) . . . . Tanytarsus
   Second antennal segment distinctly wedge-shaped, sub-equal in length to third segment; large Lauterborn organs arise from short pedicels (Fig. 5F). . . . Cladotanytarsus

5. Apex of labrum with distinct brush of setae (Fig. 5C) . . . . Xenochironomus
   Apex of labrum without such an anterior brush. 6

6. Head dorso-ventrally flattened. Ventromental plates without striae, with few hooks (Fig. 4K). 7
   Head not flattened. Ventromental plates distinct, striate (Fig. 3C-F) 8

7. Antennal 3rd segment short, same length as 5th, c 50% length of 4th (Fig. 3J). . . . . Harrisius
   Antennal 3rd segment only slightly shorter than 4th . . . . Stenochironomus

8. SI seta plumose; SII not blade-like; labral lamellae present (Fig. 3B). Pecten epipharyngis usually a wide plate, rarely reduced to three sometimes serrate lobes (Fig. 3B). 9

SI and SII setae simple, frequently blade-like; labral lamellae absent (Fig. 3E). Pecten epipharyngis usually reduced to single scale, rarely toothed . . . .
. . . . Harnischia complex 16

9. Antenna five-segmented with Lauterborn organs opposite on 2nd segment or absent (Fig. 3H,L), or four-segmented with Lauterborn organs displaced along 2nd (Fig. 4I) 10

 Antenna six-segmented with Lauterborn organs alternate, either on apices of 2nd and 3rd segments or alternate on 2nd segment (Fig. 4D,L) 13

10. Mandible with basal striations (Fig. 3A, arrowed). Body of larva generally with two pairs of ventral tubules and 1 pair of lateral tubules on posterior segments although some reduction may occur. . . . . *Chironomus*

 Mandible lacking basal striations . . . . , 11

11. Ventromental plates narrow, only c. 2 × as wide as deep (Fig. 3F). Fenestra (Fig. 3G, arrowed) may be present
. . . . *Dicrotendipes*

 Ventromental plates broad, at least 2.5 × as wide as deep (Fig. 3K). 12

12. Premandible (*pmd*) with at least 5 teeth (Fig. 4B, arrowed). Fenestra (as in Fig. 3G) on anterior frons . . *Kiefferulus*

 Premandible with 2-3 teeth. Frons without fenestra
. . . . *Polypedilum*

13. Apical segment of antenna elongate, whip-like (Fig. 5D). All mental teeth pale (Fig. 5E) . . unknown genus 'K2'

 Antennal apical segments conventionally short, not whip-like (Fig. 4D). Median mentum paler than lateral teeth, or evenly darkened. 14

14. Median part of mentum pale (Fig. 4C) . . *Microtendipes*

 Median mentum dark 15

15. Uneven number of subequal mental teeth (Fig. 5A)
. . . . *Stictochironomus*

 Even number of disparate-sized mental teeth (Fig. 3I)
. . . . *Conochironomus*

16. Mentum concave with pale median tooth (Fig. 3E)
. . . . *Cryptochironomus*

 Mentum conventionally convex 17

17. Mentum with outermost group of 3 teeth forming group distinctively set-off from general slope (Fig. 3C)
. . . . *Cladopelma*

 Mentum generally with teeth decreasing evenly in height from median to outermost 18

18. Median teeth of mentum dark, no wider than any lateral teeth. Anterior margin of ventromental plate crenulate (Fig. 4F, arrowed) . . . . *Parachironomus*

 Median teeth of mentum pale, broader than outermost teeth. Anterior margin of ventromental plate smooth (Fig. 3I). . . . . *Harnischia*

DISCUSSION

The total chironomid fauna of each Atherton Tableland lake (Barrine – 22 species, Eacham – 28 species and Euramoo – 12 species) is appreciably richer than assessed previously by larval benthic sampling (e.g. Timms, 1979). Lower numbers such as those based on grab-sampled benthos alone, gave rise to a belief that Australian lakes were species-poor relative to elsewhere. However, as observed by Wright &

Cranston (2000), exuvial sampling consistently demonstrates a more complex system, certainly including littoral taxa and those living in obscure (and under-sampled) substrates such as immersed wood. The diversity of Lakes Eacham and Barrine lies at the high end of studied lakes in Australia (Wright & Cranston, 2000), which in turn are comparably diverse to all except natural eutrophic lakes elsewhere in the world. Although modern Lake Euramoo now appears to have fewer species, historically an additional 20 taxa have occurred there (represented by subfossils), many of which are present now in either or both Lakes Eacham and Barrine.

Ordination of the chironomid fauna of Lakes Barrine and Eacham with environmental variables showed a significant correlation with water and air temperatures (Dimitriadis & Cranston, 2001). Thus different historical assemblages of chironomids (as represented by preserved head capsules) could be taken to infer different past climates. The presence of *Zavreliella marmorata*, *Thienemanniella*, *Microchironomus*, *Riethia* and ?*Skusella* sp. only amongst subfossil assemblages may reflect such differences. Cumulative species diversity through accumulation in longer time slices (as in palaeo-reconstruction) can lead to perhaps misleading impressions of higher past diversity than does the modern 'snapshot'.

The modern biota described above tends to be northern Australian to Asian outside the immediate study area, with little evidence of Gondwanan (cool/mesotherm, southern-connected) taxa.

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